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**Consistent alleviation of abiotic stress with silicon addition: a meta-analysis**

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Running title: Abiotic stress alleviation by silicon

## ABSTRACT

- Hundreds of single species studies have demonstrated the facility of silicon (Si) to alleviate diverse abiotic stresses in plants. Understanding of the mechanisms of Si mediated stress alleviation is progressing, and several reviews have brought information together. A quantitative assessment of the alleviative capacity of Si, however, which could elucidate plant Si function more broadly, was lacking.
- We combined the results of 145 experiments, predominantly on agricultural species, in a meta-analysis to statistically assess the responses of stressed plants to Si supply across multiple plant families and abiotic stresses. We interrogated our database to determine if: stressed plants increased in dry mass and net assimilation rate, oxidative stress markers were reduced, anti-oxidant responses were increased and if element uptake showed consistent changes when supplied with Si.
- We demonstrated that across plant families and stress types, Si increases dry weight, assimilation rate and chlorophyll biosynthesis and alleviates oxidative damage in stressed plants. In general, results indicated that plant family (as a proxy for accumulator type) and stress type had significant explanatory power for variation in responses. The consistent reduction in oxidative damage was not mirrored by consistent increases in anti-oxidant production, indicative of the several different stress alleviation mechanisms in which Si is involved. Silicon addition increased K in shoots, decreased As and Cd in roots and Na and Cd in shoots. Silicon addition did not affect Al, Ca or Mn concentration in shoots and roots of stress plants. Plants had significantly lower concentrations of Si accumulated in shoots but not in roots when stressed.
- Meta-analyses showed consistent alleviation by Si of oxidative damage caused by a range of abiotic stresses across diverse species. Our findings indicate that Si is likely to be a useful fertilizer for many crops facing a spectrum of abiotic stresses. Similarities in responses across families provides strong support for a role of Si in the alleviation of abiotic stress in natural systems, where it has barely been explored. We suggest this role may become more important under a changing climate and more experiments using non-agricultural species are now needed.

Keywords: stress alleviation, silica, agriculture, silicon fertiliser, oxidative stress, heavy metal toxicity

## INTRODUCTION

Plants can use silicon (Si), acquired as a nutrient through their roots, to alleviate the impacts of an impressive range of abiotic stresses including salinity, metal toxicity, nutrient imbalance, temperature and water stress (Ma 2004). Our knowledge of these functions comes from predominantly agricultural studies and in comparison, a role for Si in abiotic stress elevation in natural ecosystems has been little considered (Cooke & Leishman 2011). Abiotic stress is estimated to reduce the yield of crops by 51-82% (Bray, Bailey-Serres & Weretilynk 2000). Plants in natural systems contend with abiotic stress with seasonal variations, unusual weather, environmental gradients and at the edge of their ranges, as examples (Hirt & Shinozaki 2004). Impacts of abiotic stress are increasing; in response to rising demand, agriculture has expanded into sub-optimal areas, causing a need to ameliorate the resultant plant stresses to improve crop yield (Tilman *et al.* 2001) and a changing climate means both agricultural and native species experience altered rainfall and temperature regimes (IPCC, 2014). Abiotic stresses disrupt cellular homeostasis and increase the production of reactive oxygen intermediates (ROIs). High levels of these toxic compounds can induce cell death due to membrane, RNA and DNA damage (Mittler 2002).

The wide-ranging benefits of Si for stressed plants are exploited for agricultural gain (Datnoff, Snyder & Korndorfer 2001). Si is routinely added to a variety of crops, most notably rice and sugarcane (Korndorfer & Lepsch 2001), to increase yield (Datnoff *et al.* 2001). Using agricultural studies, Liang *et al.* (2007) identified four main mechanisms of Si use for abiotic stress alleviation: (a) stimulation of stress response systems through increased anti-oxidant production; (b) binding of Si to toxic metal ions resulting in co-precipitation and complexation; (c) changing uptake rates of toxic or scarce elements; and (d) changing the deposition or storage location of metal ions in plants, as well as (e) immobilising metal ions in the growth media, before uptake by the plant (*ex planta*). Ma and Yamaji (2008) have identified additional functions including reducing water loss through cuticular transpiration via deposition of silica beneath the cuticle and increasing the strength of stems through silica deposition. Silicon has also been shown to reduce UV-B stress (Schaller *et al.* 2013).

Hundreds of studies have now assessed the capacity of Si to alleviate abiotic stresses in single species by single stress experiments. While the responses and mechanisms of stress alleviation by Si have been qualitatively reviewed (Ma, Miyake & Takahashi 2001; Ma 2004; Liang *et al.* 2007; Balakhnina & Borkowska 2013; Adrees *et al.* 2015; Pontigo *et al.* 2015), a numerical assessment is lacking and it is not known if predictable plant use of Si in stress alleviation occurs across plant groups and different stresses. Determining if stressed plant responses to Si application are consistent and which factors explain variation in plants, may stimulate better farming practices or more efficient Si fertiliser use. From an ecological perspective, consistency of responses to Si across families could allow predictions about how plants use Si to alleviate stress in natural systems. Meta-analyses allow statistically robust comparisons across multiple studies and hypothesis testing of data combined from many experiments (Gurevitch, Curtis & Jones 2001). Here, we quantitatively assess if Si consistently alleviates abiotic stress in plants through the reduction of oxidative stress.

Most research examining the effect of Si on alleviation of abiotic stress involves single species, single stress, often factorial experiments with four treatments arising from different combinations of stressed

(+Stress) and unstressed (-Stress) plants that are treated (+Si) or untreated (-Si) with Si fertiliser, although a subset with stressed plants +/- Si is also frequent. Stresses examined include water, salinity, metal and heavy metal, low nutrient, UV, heat and cold stress. A large number of measured plant responses are reported including changes in element concentration (including Si), biomass, yield, stress indicators (especially for oxidative stress), enzymatic and non-enzymatic anti-oxidant responses, and photosynthetic and transpiration rates. Common markers of oxidative stress include hydrogen peroxide (H<sub>2</sub>O<sub>2</sub>), malondialdehyde (MDA) and proline (PRO) concentration. The dominant ROI-scavenging enzymes in plants to combat oxidative stress comprise superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) and peroxidase (POD).

Silicon is acquired through the roots of plants as silicic acid and transported up through the plant in the xylem (Raven 1983). Nodulin 26-like intrinsic proteins and other aquaporins facilitate increased Si uptake in some species, and active uptake occurs through co-operation of influx and efflux transporters (Ma *et al.* 2006; Ma & Yamaji 2015; Deshmukh & Belanger 2016). The majority of Si is ultimately deposited as amorphous silica within and between cells and once deposited silica is not remobilised (Currie & Perry 2007). There is much variation in Si accumulation among families (Hodson *et al.* 2005; Trembath-Reichert *et al.* 2015) and the differential uptake is attributed to different expression rates and locations of the aquaporins (Ma & Yamaji 2015). The Poaceae is well known as a high Si accumulating family (accumulating up to 10% Si in dry mass), while the Fabaceae and Brassicaceae are considered lower Si accumulators often accumulating <1% (Datnoff *et al.* 2001; Ma 2003).

Si accumulation capacity, or plant family as a surrogate, could be an important factor affecting how stressed plants use Si to alleviate abiotic stress. Silicon is considered most important for high accumulating families, despite acknowledgment of functional roles in species that accumulate little Si (Katz 2014). The physical functions of Si, such as cuticular deposition to reduce transpiration, may be limited to high accumulating species as a build-up of silica is required (Raven 1983; Ma & Yamaji 2006; Massey & Hartley 2009). In contrast, the impact of Si accumulation capacity on biochemical functions associated with abiotic stress alleviation, may be lower with a smaller but concurrent supply of Si may be needed (Iwasaki *et al.* 2002a). Tomatoes (*Solanum lycopersicum*), for example, are considered low-moderate accumulators of Si, but Si fertiliser alleviates salt stress, boron toxic soils and fungal infections in this species (Al-Aghabary, Zhu & Shi 2004; Heine, Tikum & Horst 2005; Romero-Aranda, Jurado & Cuartero 2006; Gunes *et al.* 2007).

Stress type could also be a factor explaining variation in how Si ameliorates abiotic stress in plants. As described above, Si is involved in multiple mechanisms of stress alleviation depending on the type of stress (Liang *et al.* 2007). An example of this is anti-oxidant activity, which shows both significant increases and decreases in production when stressed plants are supplied with Si (eg. Liang *et al.* 2003; Ma *et al.* 2004; Gunes *et al.* 2007b). Increased anti-oxidant production can be induced by Si supply, but reduced anti-oxidant production could arise from reduction of the stress through another mechanism as described above. Using tomatoes as an example again, when supplied with Si, the alleviation of salt stress was associated with a significant stimulation of anti-oxidant production (Shi *et al.* 2014), while the alleviation of boron stress was associated with reduced B uptake which resulted in a reduction of anti-oxidant production (Gunes *et al.* 2007a).

A third factor that is potentially important to consider in assessing the consistency in alleviation of abiotic stresses by Si is plant part. Differences have been noted between shoot and root responses when Si is applied to stressed plants (eg. Cocker, Evans & Hodson 1998a; Zsoldos *et al.* 2003a). For example Zsoldos *et al.* (2003b) report that Si supply to aluminium-stressed wheat led to increased accumulation of Si in roots compared with shoots. Knowledge of shoot and root responses may allow further understanding of the mechanisms by which Si alleviates such a broad range of biotic stresses, particularly in terms of storing toxic levels of metals and salts.

In addition to abiotic stress alleviation, Si is used by plants to defend against biotic stresses, particularly herbivory. In some Poaceae, sustained herbivory can induce the uptake of additional Si in both natural and agricultural systems (Reynolds, Keeping & Meyer 2009; Hartley & DeGabriel 2016). It is not known if abiotic stress induces plants to take up more Si in a similar way.

The many single species studies provide the opportunity to test for consistency across a diverse range of species and stress types. Through quantitative analysis, we first sought to definitively determine if plant biomass and photosynthesis is increased following Si supply to stressed plants, and if this consistently occurs through the alleviation of oxidative stress (ie. a reduction in oxidative stress markers). In addition, we asked if responses vary with stress type but predicted that because all stress types are likely to cause oxidative damage, stress type will not be a significant explanatory factor. We also asked if plant family, as a surrogate for Si accumulation capacity, is an important explanatory factor. Subsequently our goal was to test if there are consistent anti-oxidant responses across experiments assessing the addition of Si to stressed plants. We predicted that due to different alleviation mechanisms, there would be no clear overall signal in changes in anti-oxidant activity when stressed plants are supplied with Si. However, we anticipated that plants stressed by metals and heavy metals show a reduction in anti-oxidant production, and other stresses show a significant increase. Next we sought to test if element uptake, including toxic elements, was consistently increased or decreased in plants, across species, and if there are differences in root and shoot allocation of these elements. We predicted reduced uptake of Na and metals, with no difference between roots and shoot allocation and no impact of plant family. Finally, given that herbivory can induce increased Si uptake, we predicted that plants would take up more Si when stressed, with a stronger signal in higher Si accumulators. In summary we tested the following hypotheses:

1. Plant biomass and net assimilation rate are consistently increased following Si supply to stressed plants, with family but not stress type significant explanatory factors
2. Oxidative stress is consistently alleviated (ie. a reduction in oxidative stress markers) with family but not stress type a significant explanatory factor
3. Anti-oxidant responses are not consistent across experiments assessing the provision of Si to stressed plants, and stress type will be a significant explanatory factor because plants stressed by metals and heavy metals will show a reduction in anti-oxidant production, while other stresses will show an increase
4. Element uptake is consistently increased or decreased across plants dependent on the element, with differences in root and shoot allocation of these elements and no impact of plant family

5. Plants take up more Si when exposed to abiotic stress

**MATERIALS AND METHODS**

Identification of papers, selection of data and analysis followed a consistent approach (Koricheva & Gurevitch 2014, see Supplementary Information Table S1). To identify studies in which stressed plants were grown with and without Si fertiliser, a tailored Web of Science, BIOSIS Citation Index search was carried out on 15 August 2015 using ((alleviat\* or ameliorat\* or amend\* or contaminat\* or deficien\* or drought or enhance\* or excess\* or imbalance or induc\* or mediat\* or modifi\* or modulat\* or resistance or salin\* or stress\* or tolerance or toxic\*) not blast not borer not disease not fung\* not grazing not herbiv\* not infection not insect not mildew not root rot) AND (silicon or silica or "Si" or silicification or silicate or silicic) in the title AND (plant or leaf or leaves or shoot or root or stem or grass) in the topic. The search was further refined by selecting only journal articles and conference proceedings and including only journals likely to be relevant (including plant sciences or food science technology or chemistry physical or agronomy or biology or environmental science or ecology or soil science or chemistry multidisciplinary or chemistry analytical or agriculture multidisciplinary or biochemistry molecular biology or horticultural or forestry or agricultural engineering).

The search identified 504 papers, of which after inspection of titles and abstracts 352 were considered potentially relevant and 93% of these papers could be obtained. Papers were excluded where experimental design was not suitable for comparison (ie. did not follow experimental design of stressed plants +/- Si addition), foliage rather than root application of Si was employed, and replication details and/or measures of variance were not supplied (including by authors on request). In total, information from 145 papers was accessible, suitable, and collated for analyses. Data were extracted from figures using DataThief (Tummers 2006) and Web Plot Digitizer (Rohatgi 2015) where necessary. Only the maximum stress and Si treatment levels were selected where multiple levels were included in the experimental design, and all cultivars listed were included separately.

For each experiment, details for as many of the four potential treatments reported (-Si-Stress, +Si-Stress, -Si+Stress, +Si+Stress) were recorded, together with the sample size. Measures of variance were recorded as standard deviations, converting other measures where possible. Not all of the responses could be used in the analyses due to small sample sizes. Subsets of data, isolating the most frequently measured responses, were extracted to test specific hypotheses. Shoot or leaf responses were used in analyses of net assimilation rate, chlorophyll content, oxidative stress markers (MDA, H<sub>2</sub>O<sub>2</sub>, proline concentration) and anti-oxidant activity (SOD, CAT, POD and APX) and both shoot and root responses were used in analyses of dry weight (DW) and element content (Al, As, Ca, Cd, K, Mn, Na, Si). Although cultivars play an important role in crop selection and vary in tolerance to stresses, it was considered that species and family (a proxy for accumulator type) would have a much larger effect; hence cultivars were not included in the analyses as a factor. Values were predominantly reported for shoots of non-woody and leaves of woody species and we considered these analogous, referring to them all as shoots.

After selecting subsets of data to analyse the variables above, of the 145 studies from which we extracted information, we used data from 125 published papers (Matoh, Kairusmee & Takahashi 1986; Ma &

Takahashi 1990; Bradbury & Ahmad 1990; Ahmad, Zaheer & Ismail 1992; Barceló & Guevara 1993; Hammond, Evans & Hodson 1995; Liang *et al.* 1996, 1999, 2008; Corrales, Poschenrieder & Barceló 1997; Nowakowski & Nowakowska 1997; Cocker *et al.* 1998a; Liang 1998; Rahman *et al.* 1998; Yang *et al.* 1999; Yeo *et al.* 1999; Hara, Gu & Koyama 1999; Iwasaki & Matsumura 1999; Iwasaki *et al.* 2002b; Rogalla & Roemheld 2002; Zsoldos *et al.* 2003a; b; Gong *et al.* 2003, 2005; Gong, Randall & Flowers 2006; Gong *et al.* 2008; Al-Aghabary *et al.* 2004; Zhu *et al.* 2004; Shi *et al.* 2005b, 2010, 2013, 2014; Eneji *et al.* 2005; Guo *et al.* 2005, 2007, 2013; Hattori *et al.* 2005, 2008; Shi *et al.* 2005a; Treder & Cieslinski 2005; Tahir *et al.* 2006, 2010; Moussa 2006; Romero-Aranda *et al.* 2006; Wang & Han 2007; Gunes *et al.* 2007b; c; da; e, 2008; Maksimovic *et al.* 2007, 2012; Savvas *et al.* 2007; Murillo-Amador *et al.* 2007; Tuna *et al.* 2008; Nwugo & Huerta 2008a; b, 2011; Saqib, Zörb & Schubert 2008; Vaculík *et al.* 2009, 2012; Feng, Shi & Wang 2009; Feng *et al.* 2010; Inal, Pilbeam & Gunes 2009; Doncheva *et al.* 2009; Pei *et al.* 2009; He *et al.* 2009; Song *et al.* 2009, 2011; Ashraf *et al.* 2010b; a; Lee *et al.* 2010; Miao, Han & Zhang 2010; Chai, Shao & Zhang 2010; Shen *et al.* 2010a; b, 2014a; b; c; Hashemi, Abdolzadeh & Sadeghipour 2010; Singh *et al.* 2011; Chen *et al.* 2011; Yao *et al.* 2011; Zeng *et al.* 2011; Frantz, Khandekar & Leisner 2011; Kafi & Rahimi 2011; Tripathi *et al.* 2012a; b, 2013; Fu *et al.* 2012; Gong & Chen 2012; Gu *et al.* 2012; Li *et al.* 2012, 2015; Masarovič *et al.* 2012; Yin *et al.* 2013, 2014; Zhang *et al.* 2013a; b; Farooq *et al.* 2013; Habibi & Hajiboland 2013; Hu *et al.* 2013; Liu *et al.* 2013, 2014, 2015; Lukačová *et al.* 2013; Mateos-Naranjo, Andrades-Moreno & Davy 2013; Mateos-Naranjo *et al.* 2015; Pavlovic *et al.* 2013; Chalmardi, Abdolzadeh & Sadeghipour 2014; Siddiqui *et al.* 2014; Soundararajan *et al.* 2014; Dufey *et al.* 2014; Habibi 2014; Hajiboland & Cheraghvareh 2014; Kang *et al.* 2014; Khoshgoftarmansh, Khodarahmi & Haghighi 2014; Kim *et al.* 2014a; b; Kostopoulou & Therios 2014; Bokor *et al.* 2014; Mihaličová Malčovská *et al.* 2014; Sanglard *et al.* 2014; Sayed & Gadallah 2014; Tang *et al.* 2015; Wu *et al.* 2015; Anwaar *et al.* 2015; Gengmao *et al.* 2015; Greger *et al.* 2015; Balakhnina *et al.* 2015; Mbonankira *et al.* 2015).

Meta-analyses were conducted in Metafor in R (Viechtbauer 2010). For subsets of the data, the effect size, Hedges' *d*, for individual studies was calculated for the relevant pair of responses (-Si+Stress vs +Si+Stress for all comparisons except Si accumulation which used +Si-Stress vs +Si+Stress). This effect size measure compares two means using a pooled standard deviation and bias correction, and is a measure of the number of standard deviations by which the means differ (Hedges & Olkin 1985). A positive value indicates that the response measure was higher in the experimental versus control treatment, while a negative value indicates the response measure in the experimental treatment was lower. The data were checked for outliers and normality of residuals.

Models were analysed with the *rma.mv* function in the *metaphor* package, with a maximum likelihood "ML" model fit. Overall effect sizes ("Overall") across studies were determined using a (null) model with publication (reference) as a random factor, which accounted for similarities of results within studies. Including species as a random factor did not have additional explanatory power and hence was not included in models. To further explore the sources of heterogeneity among responses, a combination of fixed and random effects, in mixed models, were used. In these models publication as a random factor was retained and either plant family or stress type was the fixed effect. Plant family can be considered a surrogate for variation in Si accumulation capacity (Hodson *et al.* 2005). We did not assign families to specific accumulation groups as there



are not yet definitive classifications (Deshmukh & Belanger 2016), but shoot Si content from our database was compared to a larger dataset of Si accumulation for relevant families (Trembath-Reichert *et al.* 2015) to allow interpretation of the results according to accumulation potential (Supporting information Fig S1).

Interactions between family and stress type are possible and ideally we would test for the interaction of these two moderators in the same model. However, this was not possible because the data compilation did not include multiple stress types applied to the same families with sufficient numbers of samples. Instead we tested the importance of stress type as a moderator in a single family, the Poaceae, for which the most data had been collected. When stress type explained significant heterogeneity in analysis of both the full data set and the Poaceae subset, we could be more confident of a true effect of stress type. Differences among families could not be tested in the same way as there were insufficient data.

Null model results indicated if there were significant overall effects of Si addition. Mixed-effect model results indicated if family or stress type explained a significant proportion of variation (heterogeneity) among studies. If the heterogeneity explained by the model including a moderator ( $Q_M$ ) was significant, we considered the moderator likely to be an important factor. Log ratio tests, comparing null and mixed models yielded almost identical findings (data not shown). The 5-95% confidence intervals in figures were used to determine if overall effect sizes for each factor (plant family or stress type) were significantly different from zero (ie if 95% confidence intervals do not overlap zero then there is a significant overall positive or negative effect) or each other.

## RESULTS

### *Data set*

The dataset used across all meta-analyses included 16 families comprising 48 plant species (Supplementary information, Table S2). Poaceae was best represented with 15 species, Fabaceae with 10, and Asteraceae, Cucurbitaceae and Solanaceae with 3 and two species in each of Amaranthaceae and Brassicaceae. Silicon content varied between families, with the Poaceae the highest (Supplementary information, Fig. S1). The majority of species were agricultural plants, often domesticated (Supplementary information, Table S2). The majority ( $\approx 75\%$ ) of experiments used hydroponic systems while others used sands, soils, vermiculite or contaminated soils in the field. Differences between growing media, study duration and stress intensity were not tested, as there were not enough studies from the same family and same stress type to allow this.

The most frequently imposed stresses across studies were salinity ( $n=44$  papers) and water stress ( $n=22$ ) with metal (Al ( $n=17$ ), B ( $n=7$ ), Cu ( $n=3$ ), Mn ( $n=8$ )) and heavy metal stresses (As ( $n=6$ ), Cd ( $n=17$ ) and Cr ( $n=3$ )) also popular. Cold temperature, acid rain, UV-B, heat and high and low phosphorus stress were represented by 1 to 3 experiments each.

There was some evidence of publication bias, as shown by funnel plots (Supplementary Information, Fig S3) mainly for shoot and root biomass measurements, but plotting residuals of models including moderators showed less bias. Four of the 27 responses showed significant, but generally weak temporal trends (Supplementary Information, Table S3). Small sample sizes (ie few studies) for some families and stress types resulted in large confidence intervals that meant for some groups the results were not significant despite

potentially large effect sizes. In part, this illustrates the benefits of meta-analyses as the quantitative combination of studies provided more statistical power. However, methodological heterogeneity and interactions between moderators, were difficult to explore conclusively, though causes of heterogeneity were explored (Supplementary Information, Tables S1,S4). The magnitude of the stress was significantly correlated with the magnitude of recovery (Supplementary Information, Fig. S1) which has the potential to impact magnitude but not sign of effect sizes.

#### *Plant biomass and photosynthesis*

Overall, combining experiments across 18 stress types and 14 families, supplying Si to stressed plants significantly increased the dry weight of both shoots and roots (Fig. 1, Table 1), supporting hypothesis 1. Not all groupings showed a significant dry weight (DW) increase (Fig 1), though most of the 8 stress types and 7 families that did not had small samples sizes. Both stress type and family were significant moderators in explaining variation in both shoots and roots (Table 2), though there could be an interaction between stress type and plant family. However, using only experiments from a single family (Poaceae), stress type was still a significant moderator (Table 1). Several families showed significant DW increases with Si supply for both shoots and roots (Fig. 1), though contrary to expectations, the high accumulating Poaceae did not show a stronger response than other families. No significant DW decreases were found in any stress type or family after merging studies.

Meta-analyses showed that addition of Si to stressed plants significantly increased photosynthetic rate ( $A_{net}$ ) and total chlorophyll concentration (Table 1, Fig. 2A-B). Plant family was a significant explanatory factor in models of  $A_{net}$  (Table 1) and 7 of 9 families showed a positive response to Si supply. Stress type was not an important moderator overall, but did explain significant heterogeneity within Poaceae. Plant family did not have explanatory power in models of total chlorophyll content (Table 2), and neither did stress type across families, though it was a significant moderator when considering only Poaceae (Fig. 2B, Table 1). Our hypothesis (hypothesis 1) that plant biomass and photosynthesis is increased with Si addition to a stressed plant was supported, with some apparent impacts of family and stress type. The high Si-accumulating Poaceae was not different to other families.

#### *Oxidative stress markers*

Overall, Si addition to stressed plants reduced oxidative damage, as shown by significant reductions in 2 of 3 markers of oxidative stress ( $H_2O_2$  and MDA; Fig. 3A-C, Table 1). Including either family or stress type increased the explanatory power for  $H_2O_2$  and Proline (Table 1), and stress type explained significant heterogeneity for all markers when looking at studies within Poaceae. The oxidative stress marker  $H_2O_2$  was reduced by Si addition for 7 of 10 families, including the Poaceae, Fabaceae, Solanaceae and Cucurbitaceae. These are families in which Si aquaporins have specifically been identified, while the lower Si accumulating families of Brassicaceae and Asteraceae did not show significant responses (Fig. 4A). The marker MDA was also significantly reduced following Si addition in 6 of 10 families (Fig. 3B). Proline was only significantly reduced in

Poaceae, showed no change in Asteraceae and Fabaceae, despite including 12 replicates each. It showed a positive response in Cucurbitaceae, but represented one sample only (Fig 3C).

Silicon addition significantly reduced  $H_2O_2$  concentration across all 11 stress types (Fig 4A), MDA concentration was significantly reduced for 9 stress types but not As or waterlogging stress (Fig 4B) but proline concentration was varied between negative and no effect of Si addition to stressed plant among stress types. Overall, there was support, therefore, for our hypothesis 2 that Si consistently alleviates oxidative stress and that responses differed among plant families, with stress type also an explanatory factor.

#### *Anti-oxidant responses*

There was no significant overall positive or negative effect on any of the four anti-oxidant concentrations in shoots with Si supply to stressed plants (Fig. 4, Table 1). Including stress type in meta-analysis models increased the explanatory power for SOD concentration and CAT and POD activity, but not APX activity, both for the whole dataset and the Poaceae subset (Table 1). We did not find that responses to heavy metal stress were consistent. Indeed, across the 14 stress types in the analyses, no two stresses showed the same pattern in anti-oxidant changes with Si addition (Fig. 5). For example, in B stressed plants, adding Si showed significantly reduced CAT activity (no data for POD), while in water stressed plants, SOD concentration increased with no effect on the other anti-oxidants with Si addition. Therefore, these findings supported our third hypothesis of no consistent responses in anti-oxidant levels in stressed plants supplied with Si as it is strongly dependent on stress type. Although we made no predictions about the explanatory power of plant family, it was also a significant predictor explaining heterogeneity in Si induced anti-oxidant responses to abiotic stress.

#### *Element accumulation*

The overall effect sizes showed Si addition consistently increased K, and decreased Cd and Na concentrations in shoots. Similarly, it decreased As and Cd concentration in roots of stress plants, with no significant responses for Al, Ca and Mn accumulation (Fig. 5A-G). Including plant family in models of element accumulation had significant explanatory power for about half of the groups tested, predominantly those with larger sample sizes and multiple families (Table 1). The meta-analysis supported our hypothesis 4 that there are consistent changes in uptake of some elements when stressed plants are supplied with Si. Contrary to predictions, including family as a factor did increase explanatory power for the majority of elements. In addition, there were shoot and root differences, though not formally tested here. Metal concentration was not routinely reduced, though Na concentration was consistently reduced overall.

#### *Abiotic stress induced uptake of silicon*

Overall when Si supplied plants were stressed, Si accumulation in shoots was significantly reduced across studies, though accumulation in roots was not affected (Fig. 5E). For Si accumulation in shoots, both family and stress type were significant moderators, and stress type remained a significant factor when the Poaceae were analysed alone. No moderators explained substantial heterogeneity in root Si concentration in

the whole dataset or the Poaceae. The significant decrease of Si accumulation was maintained within Asteraceae and Brassicaceae, but other families did not have mean effect sizes significantly different to zero. No family showed a significant change in the accumulation of Si in roots with Si addition. We therefore rejected our final hypothesis, number 5, that plants accumulate more Si when subjected to abiotic stresses as our analysis suggests that if anything Si uptake is reduced.

## DISCUSSION

Compilation and analysis of 125 single species and single stress studies has demonstrated consistent responses to Si addition across a broad range of plant families – with Si supply significantly alleviating oxidative stress and increasing growth. Significant stress alleviation was not limited to high Si accumulating species. Responses varied between stress types, reinforcing that Si functions through multiple stress alleviation mechanisms. Increased accumulation of Si can be induced by herbivory in some Poaceae (Reynolds *et al.* 2009; Hartley & DeGabriel 2016), but there is no evidence that abiotic stress induces additional Si accumulation and in fact could do the opposite.

Silicon consistently increases productivity in diverse plant families challenged by a range of stresses (Fig. 1, Table 1) and reduces oxidative damage (Fig. 3). The pattern is upheld in a range of families, including both the high Si accumulating Poaceae, and also in Brassicaceae, Cucurbitaceae and Fabaceae which accumulate Si to lesser extents, which indicates that the benefits of Si for the alleviation of abiotic stresses are not limited to high accumulating groups. Similarly consistent increases in productivity in plants subjected to diverse stresses following Si supply (both across families and within Poaceae) reinforces that the beneficial function of Si for plants is general in nature, as championed by other researchers (Datnoff *et al.* 2001; Ma 2004; Liang *et al.* 2007).

Meta-analyses should allow comparison between families, given sufficient samples sizes within groupings, and if 95% confidence intervals among treatments do not overlap they can be considered significantly different (Gurevitch *et al.* 2001). However, due to potential interactions between plant families and stress type and because not all family-stress type combinations were included in the meta-analysis, we are cautious about drawing conclusions about among-family differences in cases with small sample sizes. Silicon uptake is strongly associated with phylogeny (Hodson *et al.* 2005), but plants also respond to silicic acid availability with uptake increasing with availability (Ma *et al.* 2001). The amount of Si required for significant stress alleviation through biochemical mechanisms has not been established, but the significant responses by low accumulators of Si shown here, suggests that a small supply of concurrent silicic acid may be sufficient (Fig. 4).

The significant Si-induced increase in the dry weight of stressed plants can be attributed at least in part to increased chlorophyll biosynthesis and photosynthetic rates (Fig. 3A and B), however it is not clear if stress-induced suppression has been relieved or if Si stimulates these processes directly. In a proteomic assay, Nwugo and Herta (2011) showed 50 Si related changes in 50 protein spots, including those associated with photosynthesis, redox homeostasis and protein synthesis, but could not determine if Si was the signaling molecule, or if these changes were secondary to other impacts of Si. Similarly, in a review of heavy metal

alleviation by Si, Wu *et al* (2013) highlighted that it can be difficult to separate interacting avoidance and tolerance responses, and the signaling and molecular role of Si in stress alleviation warrants further investigation.

The highly consistent reduction in two oxidative stress markers across families and stress types found in this analysis (Fig. 3), was not simply reflected by an increase in the production of anti-oxidant enzymes which showed much more complicated patterns among families and stresses (Fig. 4). Several mechanisms of stress alleviation by Si aside from stimulation of anti-oxidant production have been demonstrated, so lack of significant changes in SOD, CAT, POD and APX activity with Si supply to stressed plants is suggestive that another function of Si has been employed. The reduction in anti-oxidant production for Si supplied plants subjected to Al stress, for example, is compatible with Al co-precipitating with Si either in the substrate or plant, thereby removing the stress and the need for anti-oxidants (though only represented by one study). There is strong evidence for Si amelioration of Al toxicity in the soil (by the formation of alumino-silicates which are not absorbed by plants, Liang *et al.* 2007) but studies demonstrated that the addition of Si was not altering the external solution or soil properties or provided some evidence for *in planta* mechanisms (Cocker *et al.* 1998a; Cocker, Evans & Hodson 1998b; Wang, Stass & Horst 2004). Although this meta-analysis reveals patterns in plant responses, the impact of Al stress across families and any role of anti-oxidants remains elusive.

The response in accumulation of the seven elements other than Si that were considered here (Al, As, Ca, Cd, K, Mn, Na), showed no apparent differences between shoots and roots overall (non-overlapping confidence intervals, Fig. 5A-E). Across plant families, Na content was significantly reduced in shoots but not roots (Fig. 5C). The reduction in Na concentration is attributed to a suppression of transpiration rates by Si deposition of the leaf epidermis and by partial blockage of the transpiration bypass flow (Matoh *et al.* 1986). Potassium uptake is increased in shoots with Si supply to stressed plants which supports the idea that mechanisms other than changed transpiration rates are responsible for differences in ion uptake rates. Evidence of multiple alleviation mechanisms is further provided by the uptake of Mn, which is not affected by Si supply to stressed plants (Fig. 5F). Individual studies record changes in other anti-oxidants and enzymes, such as guaiacol-peroxidase activity, not examined here, together with a change in Mn distribution within the plant (Ma *et al.* 2001; Iwasaki *et al.* 2002a; Führes *et al.* 2009).

It is well recognised that plants provided with Si in experiments increase Si concentration (Epstein 1994), and increased Si accumulation can be induced by vertebrate and invertebrate herbivory (McNaughton & Tarrants 1983; Massey, Ennos & Hartley 2007; Reynolds *et al.* 2009). In contrast dehydration or ABA treatment induces rapid reduction of Si uptake and also down regulation of Si transporter genes in rice (Yamaji & Ma 2007, 2011). However, it had not been investigated whether plants take up additional Si when suffering abiotic stresses beyond this. In contrast to our prediction, when supplied with ample Si, stressed plants compared to unstressed plants accumulate less Si in shoots with no change in root Si concentration (Fig. 5F). It appears that abiotic stresses do not induce increased uptake, and it is worth noting that no increase was found in the high Si accumulating Poaceae where induced responses have been shown in response to biotic stress (Hartley & DeGabriel 2016).

Importantly, this study found consistent patterns, despite much variation in experimental conditions of the studies examined, including substrate used (hydroponics or soil), stress application method and severity, Si application quantities and methods, and experiment duration. The consistent responses, given the variation in experimental methods, suggest that these overall responses are conserved within plant parts and potentially within families. It was assumed that the direction of the effect of Si supply to stressed plants (ie. increases or decreases in response measure) would not be impacted by experiment differences, but at worst the variation between methods would lead to broad confidence intervals and lack of significance. Although the model moderators explained significant parts of the heterogeneity in the effect size, much remained unexplained (Table 1). Methodological heterogeneity is a likely source of variation, as noted above, together with other factors not tested here, such as cultivar and domestication status. The range of stresses that Si can alleviate, and the diversity of species tested is impressive, but hampers analyses because so many combinations need replications for statistical rigour.

Although the majority of these studies have been undertaken with agricultural or horticultural species, they represent taxonomically diverse groups including Poaceae, Cucurbitaceae, Brassicaceae, Solanaceae, Amaranthaceae, and nitrogen fixing Fabaceae (Supporting Information, Table S2). Consistency in responses across this phylogenetic diversity suggests that the ability of plants to use Si is widespread. Given that Si can ameliorate stress in high and low accumulators of Si, this meta-analysis provides strong evidence that in nature there are likely to be many species for which Si is an important nutrient for stress relief. While there are ecological studies exploring the function of Si and biotic stress – predominantly herbivore stress (Massey & Hartley 2006, for example) - studies of abiotic stress amelioration in nature are limited (Cooke & Leishman 2011) but have increased in recent years.

The few studies on non-agricultural species included in this meta-analysis, however, provide tantalising evidence of the role of Si in abiotic stress alleviation in ecology. Bradbury and Ahmad (1990) demonstrated that Si increased salinity tolerance in *Prosopis juliflora*. Si was shown to reduce impacts Cd stress on mangroves, where the high availability of Si in the sea-water could play a key role in the tolerance of heavy metals of mangroves (Zhang *et al.* 2013b). Kang *et al.* (2014) demonstrated a positive impact of Si on the growth of *Haloxylon ammodendron*, a woody C4 arid-zone species, in drought conditions, but in a complicated association with NaCl. Si contributes to the salt tolerance of the marsh grass *Spartina densiflora*, despite its other adaptations to salinity and may contribute to the invasive success of this weed (Mateos-Naranjo *et al.* 2013). Si also ameliorated Cu stress in the same species (Mateos-Naranjo *et al.* 2015), an illustration of the capacity of Si to alleviate multiple abiotic stresses in natural systems. In another invasive species, *Solanum nigrum*, Si was similarly shown to reduce the impacts of Cu toxicity (Liu *et al.* 2013). The benefits of Si accumulation in wetland environments have been studied in terms of increased ability to resist water currents and allow roots to better penetrate mud (Ernst, Vis & Piccoli 1995; Struyf & Conley 2008, not included in the meta-analysis). Also Querné *et al.* (2012) investigated the potential of Si to alleviate storm, salinity, heavy metal, grazing and disease stress in *Spartina alterniflora* in an ecological study, but showed that unravelling the interactions between Si accumulation and its role in alleviating simultaneous stresses is difficult. There is a clear need for more controlled experiments involving non-agricultural species.

Meta-analyses allow outcomes of multiple studies to be collated and analysed in a quantitative fashion. With hundreds of single species, single-stress studies, this field is ripe for such an evaluation. Here we analysed the 18 response variables that were among the most frequently reported, but over 200 response types were reported in the literature (Supplementary information, Table S5). Given the consistent responses found here, across families and stresses, this approach shows potential. As more data become available, it may be possible to tease apart interactions between stress types and plant family, and incorporate the severity of stress to better understand responses. This study highlights where family by stress type data are missing for different plant responses. Changes in gene expression with Si supply found only when plants are stressed (Fauteux *et al.* 2006) and proteomics analysis also offer new ways to explore how stressed plants use Si (Nwugo & Huerta 2011), through both individual and meta-analysis studies.

Time is also ripe to better understand the function of silicon in plants, particularly in the alleviation of abiotic stress. Environmental stress causes huge losses in agricultural productivity worldwide, and expanding cropping into sub-optimal areas, emission from industry, use of wastewater for irrigation and misuse of fertilisers and pesticides are increasing the stresses crops experience (Nagajyoti, Lee & Sreekanth 2010), together with a rapidly changing climate (Challinor *et al.* 2009). Silicon may be a more environmentally-friendly alternative or complementary option to the addition of conventional fertilisers (Beman, Arrigo & Matson 2005). In addition, many Si fertilisers are made from mining waste (ie. slag) or natural products such as diatomaceous earths (Datnoff *et al.* 2001), and there is no record of too much Si causing damage to plants (Ma *et al.*, 2001). However, the increasing scale of high-Si accumulating crops means that Si use in agriculture will not be without some environmental consequences. Silicon accumulation in crops is projected to increase by up to 35% by 2050, with potential impacts on Si cycles, including increases in the relatively labile plant Si pool causing changes in dissolved Si in rivers, for example (Carey & Fulweiler 2015).

Similarly this topic and meta-analysis are timely given concerns about the adaptive potential of plants in a changing climate (Jump & Penuelas 2005). The capacity of Si to alleviate a range of abiotic stresses, including climate related stresses such as drought, high and low temperatures, could mean that Si plays an increasing role in ecological systems. We have shown that silicon consistently increases growth through the reduction of oxidative damage in plants facing abiotic stresses, and the many studies qualitatively combined here suggest that Si plays a more significant role in plant abiotic stress alleviation in ecology than currently appreciated. Controlled experiments examining these functions are likely to be illuminating and valuable.

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501 **DATA ACCESSIBILITY**

502 Effect sizes for data used in these analyses are deposited in the Dryad repository

503 (<http://datadryad.org/resource/doi:10.5061/dryad.538f8>) (Cooke and Leishman 2015)





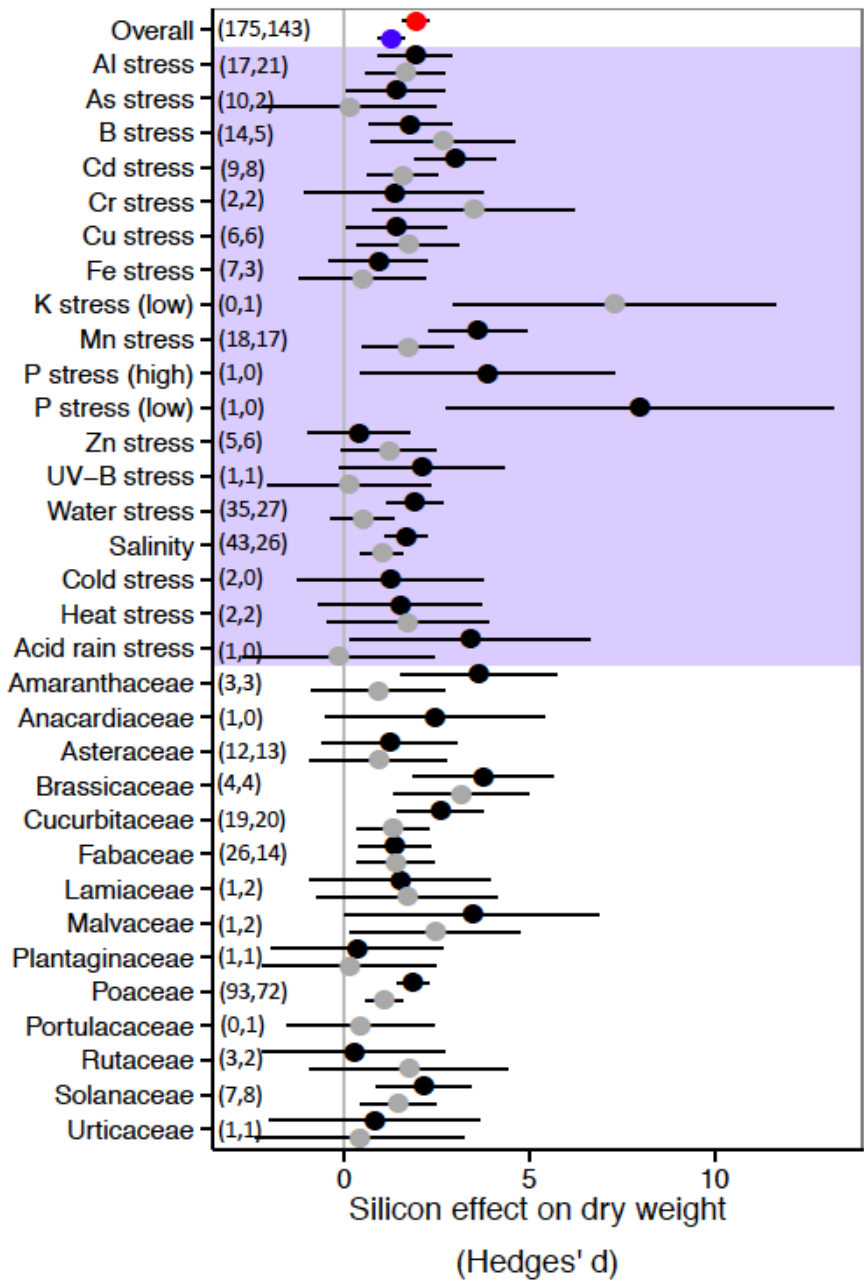
<b>SOD concentration</b> (shoots)	NA	82	50	401	453	<0.001	0.7	0.494		
	Family	82	10,71	395	332	<0.001			<b>29</b>	<b>0.001</b>
	Stress	82	11,70	405	333	<0.001			<b>22</b>	<b>0.025</b>
	(Poaceae) NA	28	1,27	129	164	<0.001	7.7	0.401		
	(Poaceae) Stress	28	7,20	135	94	<0.001			8	0.293
<b>CAT activity</b> (shoots)	NA	86	1,85	578	411	<0.001	0.61	0.543		
	Family	86	9,76	446	345	<0.001			39	<b>&lt;0.001</b>
	Stress	86	13,72	454	286	<0.001			52	<b>&lt;0.001</b>
	(Poaceae) NA	33	1,32	158	139	<0.001	0.8	0.438		
	(Poaceae) Stress	33	9,23	143	62	<0.001			77	<b>&lt;0.001</b>
<b>POD activity</b> (shoots)	NA	20	1,19	126	143	<0.001	-1.5	0.123		
	Family	20	5,14	121	91	<0.001			22	<b>0.004</b>
	Stress	20	8,11	109	50	<0.001			61	<b>&lt;0.001</b>
	(Poaceae) NA	9	1,8	44	46	<0.001	-1.2	0.226		
	(Poaceae) Stress	9	4,4	31	5	0.342			41	<b>&lt;0.001</b>
<b>APX activity</b> (shoots)	NA	66	1,65	323	346	<0.001	1.8	0.080		
	Family	66	8	307	231	<0.001			32	<b>&lt;0.001</b>
	Stress	66	10	332	263	<0.001			10	0.323
	(Poaceae) NA	27	1,26	142	165	<0.001	<b>2.4</b>	<b>0.014</b>		
	(Poaceae) Stress	27	8,18	152	135	<0.001			8	0.419
<b>Element accumulation</b>										
<b>Al</b> (shoots)	NA	18	1,17	201	152	<0.001	-1.2	0.128		
	Family	18	2,16	183	131	<0.001			.04	0.84
<b>Al</b> (roots)	NA	26	1,25	174	258	<0.001	-1.5	0.634		
	Family	26	2,24	170	222	<0.001			<b>7.8</b>	<b>0.005</b>
<b>As</b> (shoots)	NA	15	1,14	76	64	<0.001	-1.7	0.091		
	Family	15	1,13	77	57	<0.001			7.3	0.240
<b>As</b> (roots)	NA	11	1,10	52	38	<0.001	<b>-2.7</b>	<b>&lt;0.001</b>		
	Family	11	1,9	52	24	0.005			3.3	0.069
<b>Ca</b> (shoots)	NA	17	1,16	71	54	<0.001	1.2	0.224		
	Family	17	5,11	66	31	<0.001			<b>11</b>	<b>0.002</b>
<b>Ca</b> (roots)	NA	15	1,14	72	53	<0.001	0.98	0.327		
	Family	15	4,10	77	50	<0.001			4.0	0.450
<b>Cd</b> (shoots)	NA	26	1,25	131	107	<0.001	<b>-3.0</b>	<b>0.003</b>		
	Family	26	7,9	125	63	<0.001			<b>26</b>	<b>0.001</b>
<b>Cd</b> (roots)	NA	17	1,16	113	114	<0.001	<b>-2.4</b>	<b>0.017</b>		
	Family	17	9,17	97	57	<0.001			<b>33</b>	<b>0.001</b>
<b>K</b> (shoot)	NA	38	1,37	198	261	<0.001	<b>3.2</b>	<b>0.001</b>		
	Family	38	8,29	207	219	<0.001			7.7	0.486
<b>K</b> (root)	NA	25	1,24	163	194	<0.001	1.3	0.204		
	Family	25	7,18	161	134	<0.001			<b>19</b>	<b>0.007</b>
<b>Mn</b> (shoots)	NA	33	1,32	184	131	<0.001	0.22	0.801		
	Family	33	3,29	189	115	<0.001			1.5	0.683
<b>Mn</b> (roots)	NA	22	1,21	127	77	<0.001	-1.5	0.142		
	Family	22	2,19	130	75	<0.001			0.5	0.768
<b>Na</b> (shoot)	NA	52	1,51	271	276	<0.001	<b>-3.4</b>	<b>&lt;0.001</b>		
	Family	52	8,42	271	185	<0.001			<b>23</b>	<b>0.001</b>
<b>Na</b> (root)	NA	20	1,19	85	82	<0.001	-1.1	0.281		
	Family	20	6,12	91	55	<0.001			7.4	0.281
<b>Si</b> (shoots)	NA	77	1,76	450	459	<0.001	<b>-2.0</b>	<b>0.040</b>		
	Family	77	8,68	442	409	<0.001			<b>26</b>	<b>0.001</b>
	Stress	47	10,36	282	237	<0.001			<b>41</b>	<b>&lt;0.001</b>
<b>Si</b> (roots)	(Poaceae) NA	47	1,46	296	333	<0.001	-0.9	0.346		
	(Poaceae) Stress	47	10,36	282	236	<0.001			<b>40</b>	<b>&lt;0.001</b>
	Family	54	1,53	270	239	<0.001	-0.7	0.481		
	Family	54	7,46	277	201	<0.001			8	0.330

	Stress	54	9,44	281	213	<0.001		7	0.630
(Poaceae)	NA	38	1,36	188	165	<0.001	-	0.888	
							0.14		
(Poaceae)	Stress	38	9,28	196	130	<0.001		11	0.281

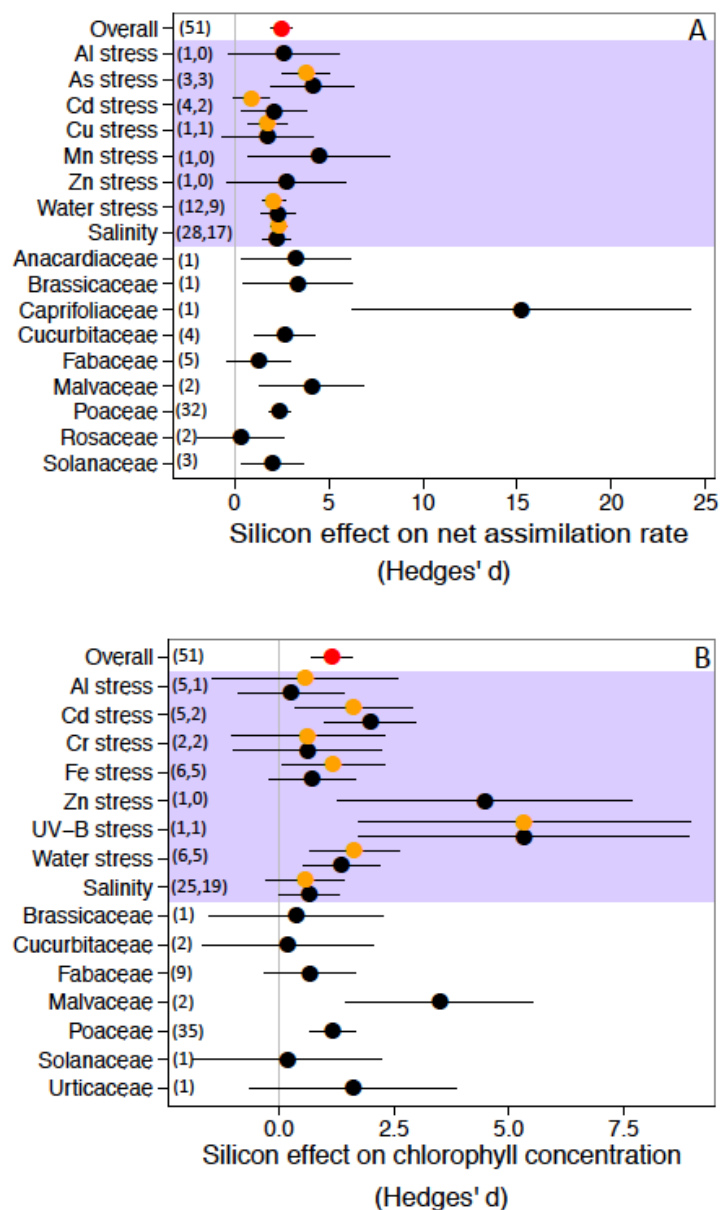
513 Hydrogen peroxide concentration ( $H_2O_2$  concentration), malondialdehyde (MDA) concentration, non-enzymatic  
514 antioxidants (AA) activity, lipoxygenase (LOX) activity, ascorbate peroxidase (APX) activity, catalase (CAT)  
515 activity and superoxide dismutase (SOD) concentration.

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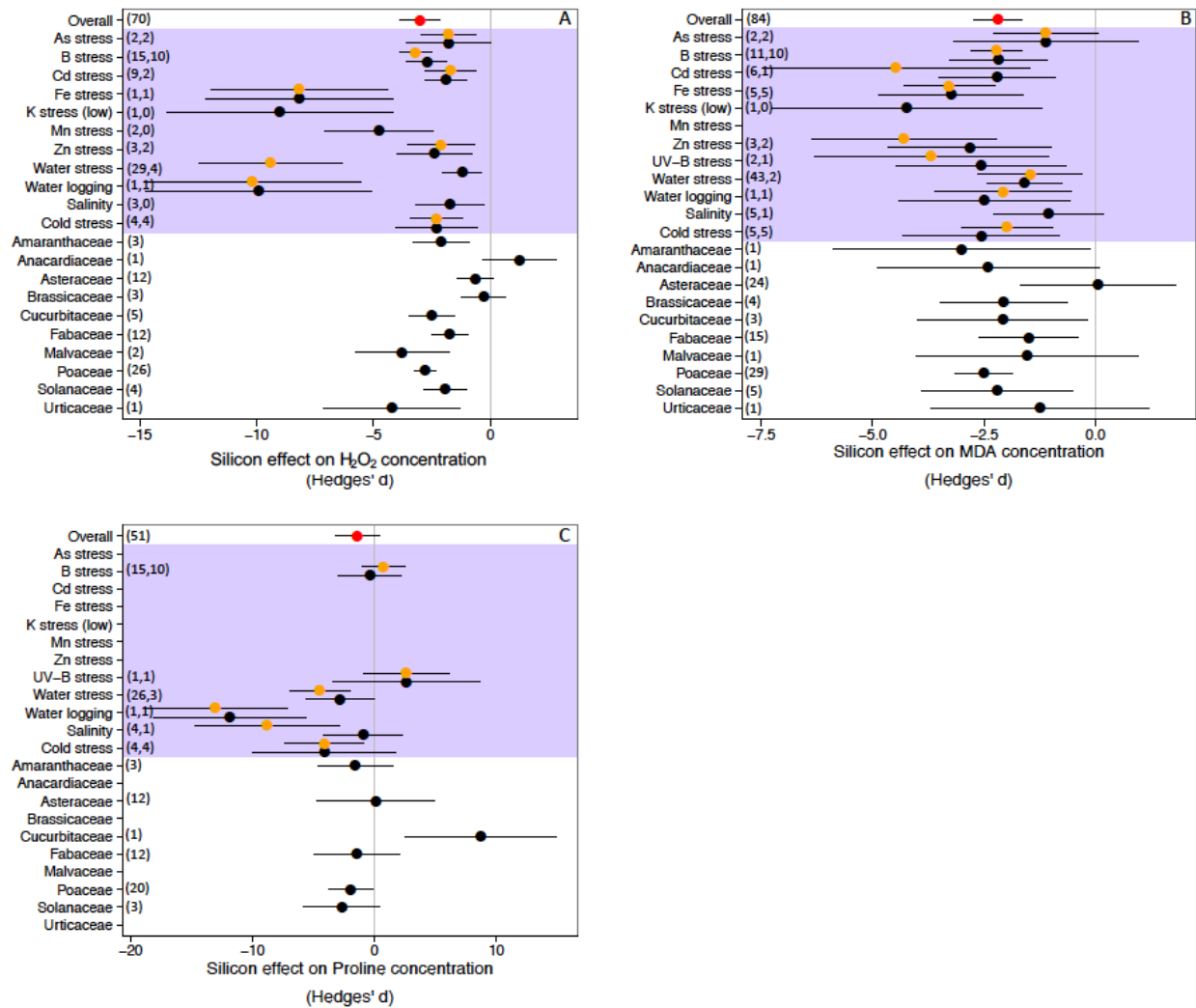
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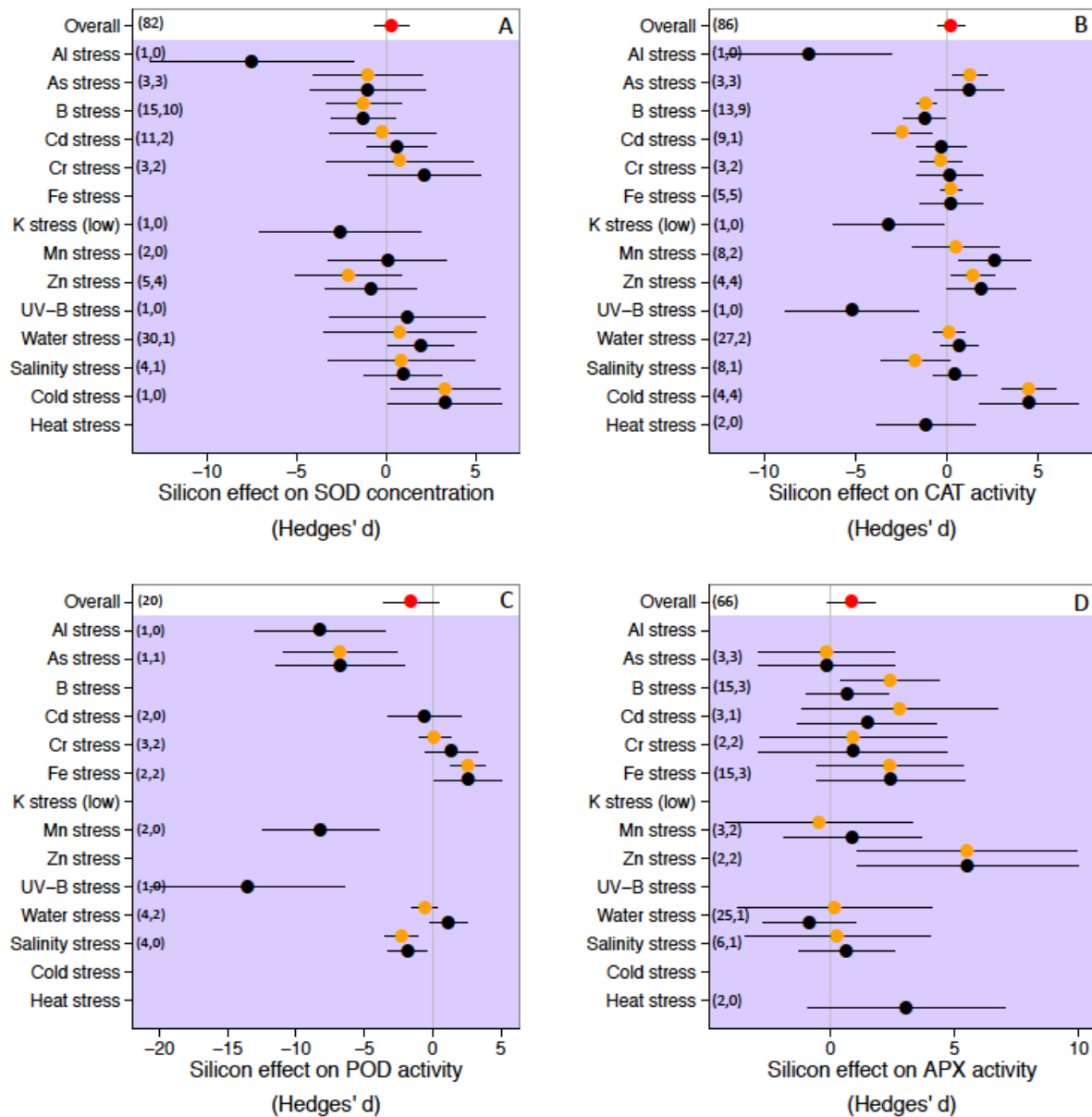
**Figure 1:** Plot of standardized effect sizes for the Si effect on dry weight. Red and blue dots indicate the mean (summary) effect size of all studies for shoot and root responses respectively. Black and grey dots indicate the mean effect sizes for factor groups of shoot and root responses respectively. Lines are 95% confidence intervals and the grey vertical line shows zero effect. Blue boxes indicate responses categorized by stress type. Samples sizes are given (shoots, roots).



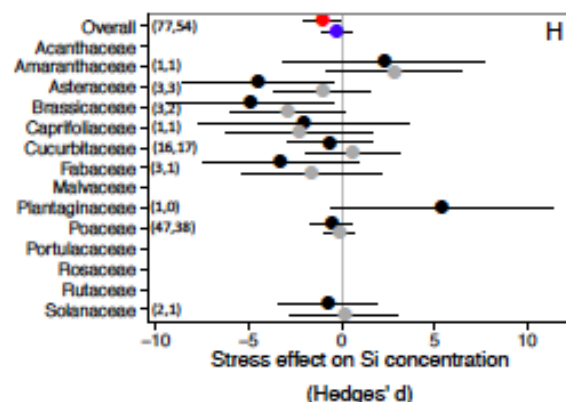
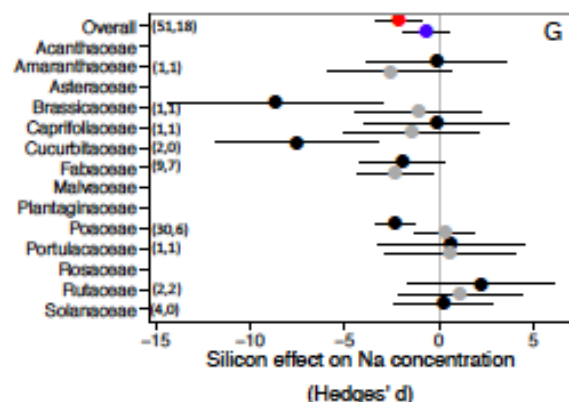
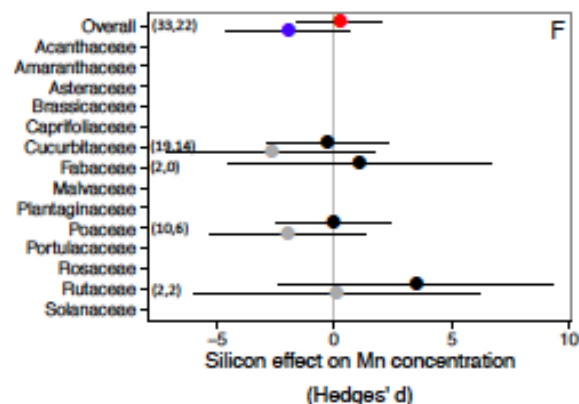
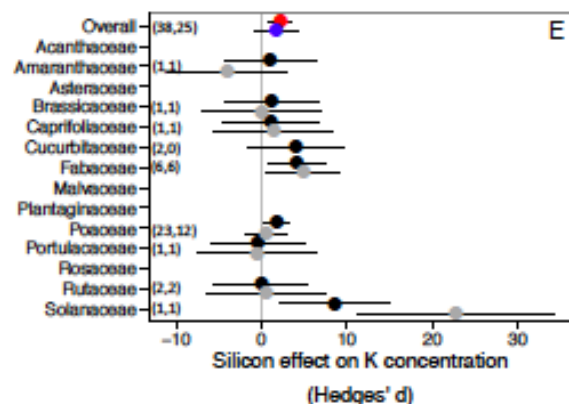
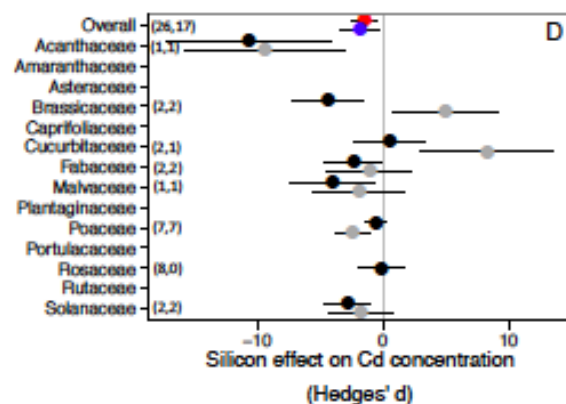
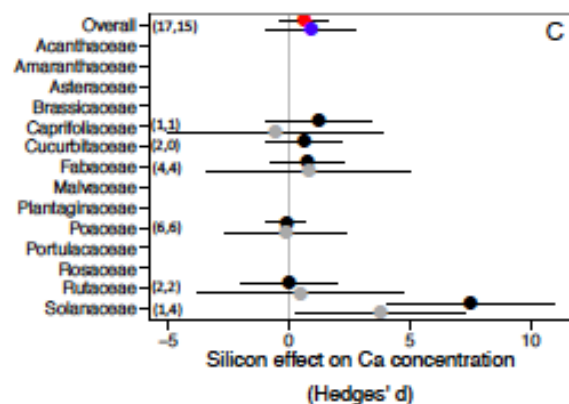
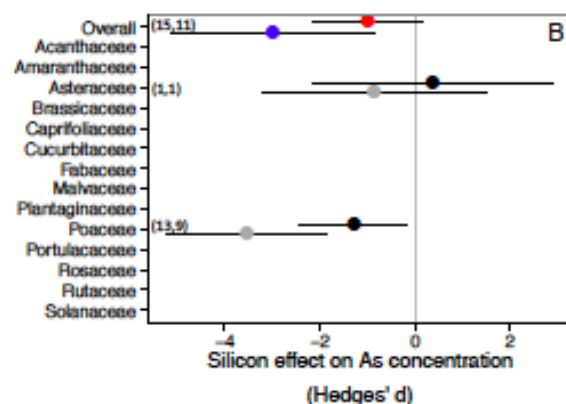
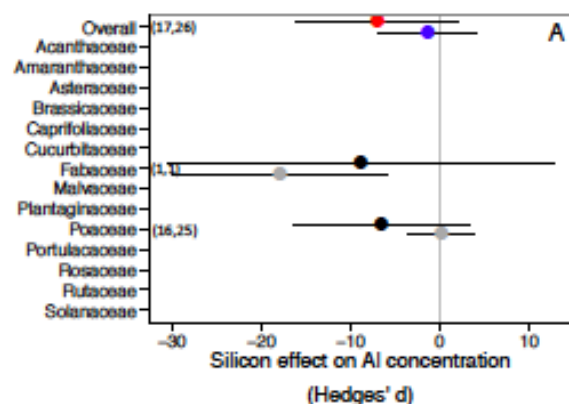
**Figure 2:** Plots of standardized effect sizes for the Si effect on (a) net assimilation rate and (b) total chlorophyll concentration in stressed plants. Red dots indicate the mean (summary) effect size of all studies, black are subsets as shown, and orange for subsets of Poaceae only. Lines are 95% confidence intervals and the grey vertical line shows zero effect. Samples sizes are given (all groups, Poaceae only).



**Figure 3:** Plots of standardized effect sizes for the Si effect on oxidative stress markers in stressed plants including (a)  $H_2O_2$  concentration; (b) MDA concentration; and (c) proline concentration. Red dots indicate the mean (summary) effect size of all studies for shoot responses. Black dots indicate the mean effect sizes for factor groups of shoot responses, and orange for subsets of Poaceae only. Lines are 95% confidence intervals and the grey vertical line shows zero effect. Blue boxes indicate responses categorized by stress type. Samples sizes are given (all groups, Poaceae only).



**Figure 4:** Plots of standardized effect sizes for the Si effect on anti-oxidant activity of stressed plants including (a) SOD concentration; (b) CAT activity; (c) POD activity and (d) APX activity. Red dots indicate the mean (summary) effect size of all studies for shoot responses. Black dots indicate the mean effect sizes for factor groups of shoot responses. Lines are 95% confidence intervals and the grey vertical line shows zero effect. Blue boxes indicate responses categorized by stress type.





**Figure 5:** Plots of standardized effect sizes for the Si effect on element accumulation of stressed plants (a) Al; (b) As; (c) Ca; (d) Cd; (e) K; (f) Mn; and (g) Na. Plot (h) shows the standardized effect sizes for the stress effect of Si accumulation in plants. Red and blue dots indicate the mean (summary) effect size of all studies for shoot and root responses respectively. Black and grey dots indicate the mean effect sizes for factor groups of shoot and root responses respectively. Lines are 95% confidence intervals and the grey vertical line shows zero effect.

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**SUPPORTING INFORMATION** Additional supporting information may be found in the online version of this article.

Table S1: Description of how the criteria for meta-analyses in ecology (Koricheva & Gurevitch 2014) were addressed in this study.

Table S2: Species and families included in the meta-analyses

Table S3: Relationships between effect size and year of publications for any of the plant responses explored in the meta-analysis.

Table S4:  $I^2$  values (%) from the null models and models with stress and family as moderators.

Table S5: Plant responses measured in the studies and collated for meta-analysis. All responses are shown to illustrate the range and diversity of information available, however not all responses were considered in the analyses.

Table S6: Studies used in the meta-analyses described in Table 1 in the main text.

Figure S1: Comparison of shoot Si content by family where given in studies compiled (filled boxes), compared to the same families from the largest current dataset of Si accumulation (open boxes), compiled by Trembath-Reichert *et al.* (2015).

Figure S2: There was a significant relationship between the impact of the stress (-Si+Stress compared to -Si-Stress, y axis) and the response to Si addition to stressed plants (+Si+Stress compared to -Si+Stress, x axis) on shoot DW, (n=155,  $R^2=0.799$ ,  $p<0.001$ ).

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